Systematics of the Garter Snake *Thamnophis atratus* at the Southern End of Its Range

by

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Variation in populations of *Thamnophis atratus*, south of the range of *T. a. hydrophilus*, was examined through multivariate analysis of nineteen characters among seven geographic units. A phylogenetic analysis of five population groups was performed using 24 characters, resulting in a single, most parsimonious tree. Variation in scalation, color pattern, tooth counts, and head morphology suggested the presence of two taxa south of the range of *T. a. hydrophilus*: typical *T. a. atratus* was restricted to California's Santa Cruz Mountains, while other central California Coast Range populations were described as a new subspecies. *Thamnophis a. aquaticus* was found to represent populations intermediate between *T. a. atratus* and *T. a. hydrophilus*, and is synonymized as a representative of an intergrading, non-diagnosable population. Ecological observations found differences in habitat use and seasonal activity between coastal and inland populations. A biogeographical model was proposed for the derivation of the subspecies, and a new subspecies, *T. a. zaxanthus*, is defined.

Resolution of garter snake (*Thamnophis*) systematics in western North America has proven to be a complicated process that is incomplete. *Thamnophis atratus* is a polymorphic species ranging from southwestern Oregon to the coast of central California (Rossman et al. 1996). Several systematic problems are unresolved within *Thamnophis atratus*, including interpretation of clinal variation within the species, status of *Thamnophis atratus aquaticus* (Rossman and Stewart 1987), and taxonomic identity of the inland, three-striped morph of *T. a. atratus* (Fox 1951). Fox (1951) analyzed variation within the species and defined three subspecies based on north-south character shifts. He included all three taxa within Fitch's (1940) *hydrophilus* group (= aquatic morph; *Thamnophis couchii* complex of Rossman and Stewart 1987 [*T. couchii, T. hammondii, T. gigas, T. atratus*]). Fitch (1940) characterized the aquatic morph, including *T. a. hydrophilus*, as having reduced or indistinct striping, an obscure, spotted pattern, subdued colors, an elongate, pointed muzzle, reduced size of posterior supralabials reflecting reduced salivary glands, relatively large eye, small pupil, and pale iris. In contrast, Fitch's (1940) *elegans* and *ordinoides* groups (= terrestrial morph; *T. elegans, T. ordinoides, T. a. atratus*) were characterized by bold striping on a black background, bright yellow throat and dorsal stripes, relatively blunt muzzle, increased height of posterior supralabials, relatively small eye, large pupil, and dark iris. *Thamnophis a. atratus* has been thought to exhibit some characters convergent with the terrestrial morph (Fox 1951; Bellemin and Stewart 1977). A third subspecies, *T. a. aquaticus* (Fox 1951), occurs between *T. a. atratus* and *T. a. hydrophilus* immediately north of San Francisco Bay, and displays characteristics intermediate between the other two subspecies. Fox (1951) reported intergrades between adjoining subspecies. Rossman and Stewart (1987) considered

T. a. aquaticus to be weakly differentiated morphologically from *T. a. hydrophilus*, and molecular studies by Lawson and Dessauer (1979) reflected this conclusion.

Variation is exhibited within each subspecies of *Thamnophis atratus*. Fitch (1940), Fox (1951) and Rossman (1979) detailed variation within *T. a. hydrophilus*, and Rossman and Stewart (1987) provided details for *T. a. hydrophilus* and *T. a. aquaticus*. Rossman (1979) and Rossman and Stewart (1987) showed that *T. a. hydrophilus* is polymorphic with respect to color pattern, having distinctly spotted and striped snakes occurring through much of the range. Fox (1951) detailed variation in *T. a. atratus* and found it to comprise two morphs: "blue-black," single-striped snakes on the San Francisco Peninsula, and three-striped snakes inland and from coastal Monterey County. He found this variation "difficult to explain," and did not define the two color morphs as subspecies. I observed that these two color morphs exist on either side of the Santa Clara Valley, with intermediates occurring at the southern end of the Santa Cruz Mountains. This observation prompted me to conduct a multivariate analysis of morphological variation in *T. a. atratus* and *T. a. aquaticus* to determine whether or not the current delineation of these subspecies is accurate. I tested the hypothesis that variation within *T. atratus* reflects a partial shift from an aquatic to a terrestrial morphotype, using sympatric *Thamnophis elegans* as the model for the terrestrial morph. Analyses of variation in *T. a. hydrophilus* (Fitch 1940; Fox 1951; Rossman and Stewart 1987) precludes the necessity of reevaluating northern populations of *T. atratus*.

MATERIALS AND METHODS

A total of 1054 snakes, both live (including field observations) and preserved, was examined from the southern half of the distribution of *Thamnophis atratus* (south of Mendocino, Lake, and Colusa counties, California). Specimens were examined in the collections of the California Academy of Sciences (CAS, CAS-SU), California Polytechnic State University, San Luis Obispo (CPS), Louisiana State University Museum of Natural Science (LSUMZ), Museum of Vertebrate Zoology (MVZ), San Jose State University (SJSU), University of California, Santa Barbara (UCSB), and National Museum of Natural History (USNM; see Appendix A and B). From 1969 through 1994, 506 *T. atratus* were observed in the field. Coloration, pattern, and ecological notes were recorded for each, and all but 63 snakes were released. Four gravid females, were kept alive until parturition. These, their offspring, and the other retained snakes were preserved and deposited in SJSU or CAS.

Only snakes over 350 mm SVL, the approximate minimum adult snout-vent length (Rossman 1979), were used for the multivariate analysis to assure that ontogenetic growth of cephalic features had approached the asymptote. Gape length was measured to the nearest 0.1 mm. Counts were made of ventrals, subcaudals, preoculars, postoculars, supralabials, infralabials, and temporals. Anterior scale rows were counted at the tenth ventral scale posterior to the chin shields. Midbody scale rows were counted halfway between occiput and vent. Posterior scale rows were counted at the antepenultimate ventral.

Vertebral stripe width was measured in number of scale rows covered at the widest part of the nuchal area (anterior stripe width), and at a point about one-third the distance from snout to vent (midbody stripe width). A ranked value (stripe value) was derived from relative visible intensity of the lateral stripe, if present, and intensity of ventral dark pigment. Because these characters were correlated, only the single ranking was necessary. Dark snakes with only a vertebral stripe were given the lowest value of 1 (Fig. 1f), while three-striped snakes with pale labials and venter received the highest value, 5 (Fig. 1d, h). Color patterns shown in Fig. 1e and 1g were ranked 2 and 4, respectively.

Clinal trends in cephalic proportions were compared through the following six ratios: antepenultimate supralabial width/height (to eliminate contour curvature of the supralabials, the stratum corneum was removed and measured on a flat surface); internasal median suture length/combined internasal posterior width; left internasal-rostral contact/combined nasal-rostral contact (after Fitch
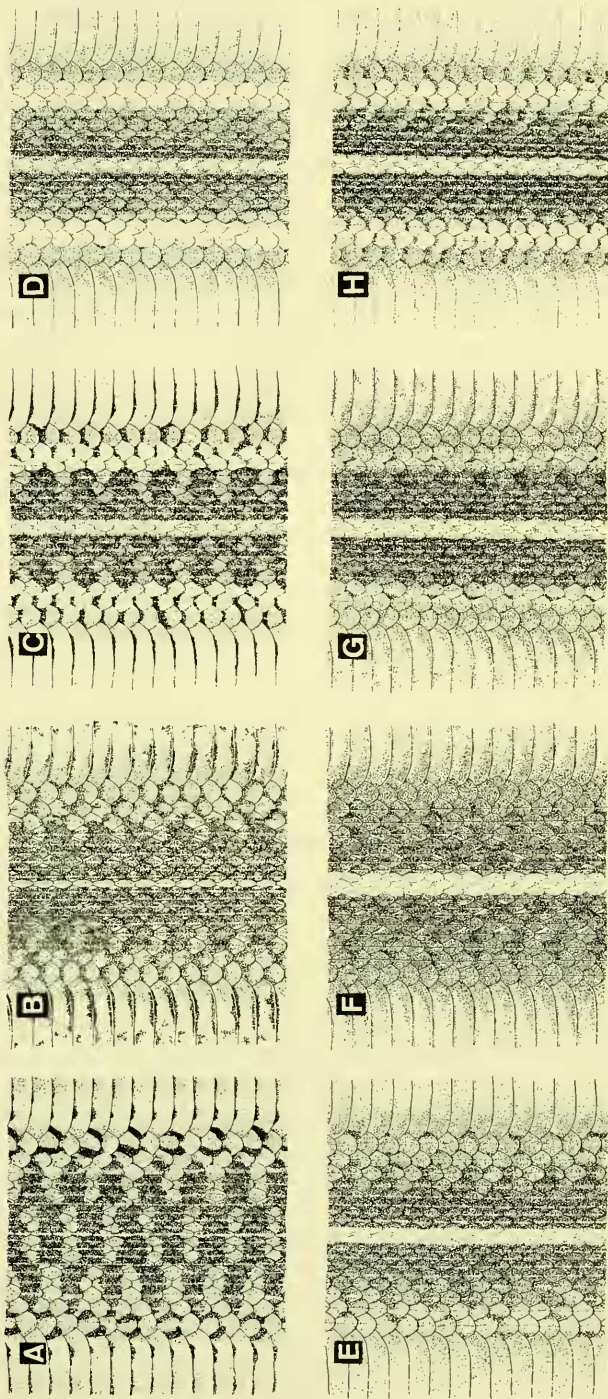
FIGURE 1. Dorsal patterns of *Thamnophis atratus*: (A) *T. a. hydrophilus*, Jackson Co., Oregon (MVZ 17425, topotype); (B) *T. a. hydrophilus*, Colusa Co., California (CAS 191546); (C) *T. a. hydrophilus*, Trinity Co., California (MVZ 42527); (D) basal *T. a. zaxanthus*, Napa Co., California (CAS 191544, "*aquaticus*" pattern); (E) basal *T. a. atratus*, San Mateo Co., California (MVZ 47923); (F) *T. a. atratus*, San Mateo Co., California (CAS 191646); (G) *T. a. atratus* × *T. a. zaxanthus* intergrade, Santa Cruz Co., California (CAS 191572); (H) *T. a. zaxanthus*, Santa Clara Co., California (MVZ 207940, holotype).

1940); anterior chin shield length/posterior chin shield length (greatest length of each shield); eye diameter/gape length; interocular width/gape length. A seventh ratio compares tail length to total length.

Specimens of *T. atratus* examined from Lake and Colusa counties, and north of the Gualala River, Sonoma County, were referrable to *T. a. hydrophilus* as defined by Fox (1951) and Rossman and Stewart (1987), and determined the northern limit of the area considered in the present paper. Southern *Thamnophis atratus* populations were divided into seven geographic samples for geographic analysis (Fig. 2). Five areas were selected because they were isolated from each other due to the presence of San Francisco Bay or naturally uninhabited valleys (Sonoma, Santa Clara, and Salinas). Two additional areas (C and E) are annectant to Area D, but were considered separately due to *a priori* recognition of intermediate or sympatric color pattern morphs in those regions. Hartley's Fmax test was used to insure homogeneity of variances for each population and each character. Area A includes all of Marin County, and Sonoma County west of the Russian River and Sonoma Valley. Area B includes the Coast Range of Napa and western Solano counties. Area C includes the San Francisco Peninsula north of Half Moon Bay and San Andreas Reservoir. Area D includes southern and central San Mateo County and the Santa Cruz Mountains south to the San Lorenzo River and Guadalupe Creek watersheds. Area E includes the southeastern flank of the Santa Cruz Mountains north to the Alamitos Creek watershed. Area F includes the Diablo Range. Area G includes the Santa Lucia and San Rafael mountains from Monterey to Santa Barbara counties. Areas A and B are currently referable to *T. a. aquaticus*, and Areas C–G to *T. a. atratus*.

The morphological data were tested for concordance with geographical distribution. A multivariate analysis was performed with the SYSTAT Discriminant Function program (Wilkinson 1988). One hundred-eighteen adult males and 115 adult females were utilized for the MANOVA. Character correlation was determined by Pearson correlation matrix using SYSTAT. The BIOSTAT t-test application (Pimentel and Smith 1986) was used to determine significance of sexual dimorphism for each character. Additional morphological analyses were performed with STATVIEW II (Feldman et al. 1986).

Phylogenetic relationships of populations in areas were evaluated with the branch-and-bound option of PAUP version 3.1 (Swofford 1993), using ACCTRAN optimization. *Thamnophis a. hydrophilus* was used as the outgroup because it is the sister taxon to southern populations of *T. atratus* (Lawson and Dessauer 1979). The use of phylogenetic trees is applicable because I believe southern populations of *T. atratus* evolved in a hierarchical fashion (see Biogeography). However, Areas C and E were left out of the phylogenetic analysis because they proved to be intermediate or mixed populations that would not conform to terminal taxa in a phylogeny. To enhance phylogenetic tree resolution several additional characters were used, including maxillary tooth count and the following ratios: pupil diameter/eye diameter, posterior frontal width/anterior frontal width, ventral margin length of sixth supralabial/length of seventh supralabial, combined internasal and prefrontal median suture length/frontal length, frontal length/parietal length, dorsal/ventral length of loreal, and prefrontal median suture length/internasal median suture length. Two ranked characters were also examined: ground color, ranked from medium gray or brown (= 3) to black (= 5), and, the projected angle formed by the suture between the sixth and seventh SL (1 = through eye, 2 = to posterior margin of eye, 3 = to posterior margin of postoculars, 4 = roughly vertical). Character means are provided in Table 1. These data were obtained from specimens in the LSUMZ collection (Appendix B), and from data in Rossman and Stewart (1987). Character states were ordered on a scale in proportion to the magnitude of difference between character means (Thiele 1993): the smallest observed distance between any pair of means was given a distance of one, and all other pairwise distances were coded relative to the smallest distance. This method preserves evolutionary information from continuous variables, and was analyzed using the step matrix procedure in PAUP.
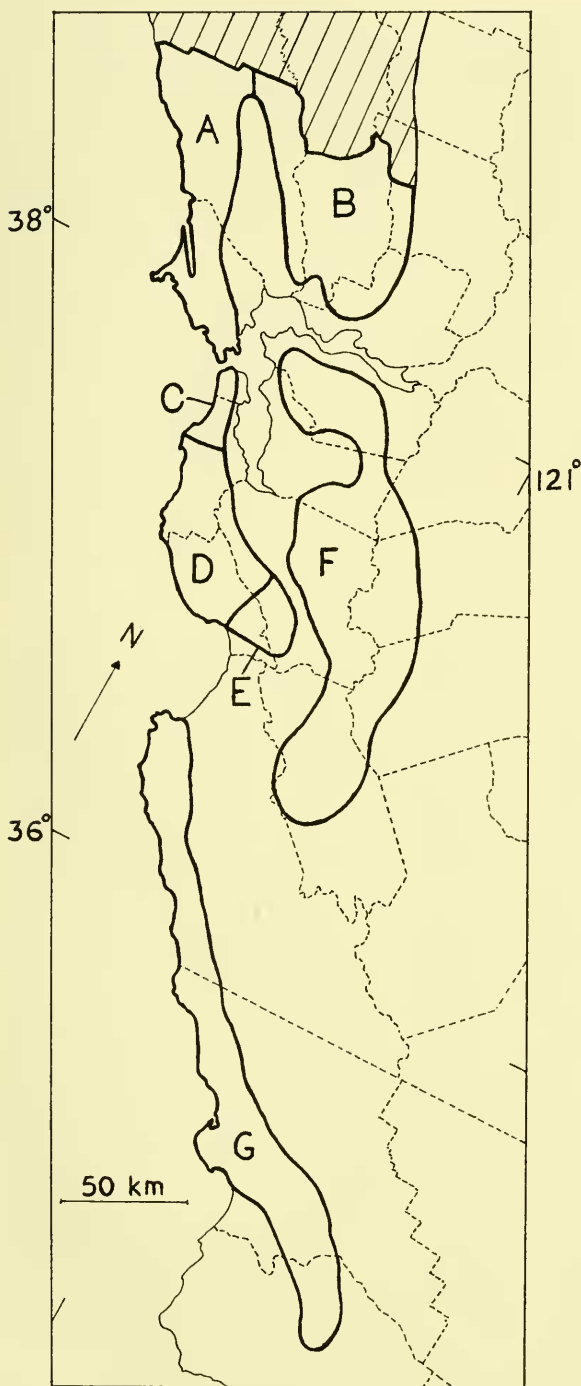
FIGURE 2. Population samples of *Thamnophis atratus* used for analyses (Areas A-G) in central California; lined area represents approximate distribution of *Thamnophis a. hydrophilus*.

The test of convergence between *Thamnophis a. atratus* and *T. elegans terrestris* was performed by alternatively constraining trees which would compare *T. e. terrestris* (convergence) or *T. a. hydrophilus* (non-convergence) as sister taxon to southern *T. atratus* populations. The latter arrangement is supported by allozyme and DNA sequence analyses (de Queiroz and Lawson 1994). Morphological data for *T. elegans* was obtained from LSUMZ specimens (Appendix B) and from Bellemin and Stewart (1977).

RESULTS

SEXUAL DIMORPHISM.—Prior to ANOVA, sexual dimorphism was examined to ensure statistical homogeneity (Thorpe 1989). Sixteen characters were analyzed using Student's t-test, eight of which were significantly dimorphic (Table 2). Thirteen non-correlated characters were examined for sexual dimorphism by discriminant function analysis: predicted vs. actual assignment resulted in 112 (97.4%) of 115 correct female assignments, and 115 (97.5%) of 118 correct male assignments ($F = 63.506$, $df = 13$, 219, $p<0.001$). Significant sexual dimorphism in half of the characters tested necessitated separate multivariate analyses for males and females.

Female SVL increased at a greater rate than that of males (Fig. 3; comparing largest male with largest female and progressively comparing pairs of smaller snakes). The ratio of mean male/female snout-vent length for each area is A = 0.96, B = 0.83, C = 0.92, D = 0.88, F = 0.88, and G = 0.86. Only three adult females were available from Area E.

TOOTH COUNTS.— Maxillary teeth, per side, were not significantly different between sexes: male range 23–27 (mean 25.3, n = 46), female range 21–28 (mean 25.2, n = 42). Tooth counts were significantly different between areas ($F = 5.64$ at 5, 95 df, $p<0.0001$), but not between areas

TABLE 1. Character means for *Thamnophis elegans* and six population groups of *T. atratus* used for phylogenetic analyses. Abbreviations: ACS/PCS, anterior/posterior chin shield length; ASR, anterior scale rows; ED, eye diameter; FL, frontal length; GL, gape length; INL, internasal median suture length; INR, internasal-rostral contact length; IOW, interorbital width; LDL/VL, loreal dorsal/ventral lengths; M/F SVL, male/female snout-vent length ratio; ML, muzzle length; MVSW, midbody vertebral stripe width; NR, nasal-rostral contact length; PD, pupil diameter; PFW/AFW, posterior/anterior frontal width; PL, parietal length; PrF, prefrontal median suture length; PSR, posterior scale rows; SC, subcaudals; SL6/SL7, ventral lengths of supralabial 6/supralabial 7; SLW/H, sixth supralabial width/height; STR, stripe value; SVL, snout-vent length; TL; tail length; TTL, total length; V, ventrals.

		Six population groups of *T. atratus*					*T. elegans*
	T. a. hydro-philus	Area A	Area B	Area D	Area F	Area G	
SVL (mm)	466.5	380.3	407.4	392.7	415.3	400.0	467.0
V	164.2	157.1	161.1	153.4	159.5	153.3	158.0
SC	86.6	83.8	82.7	79.4	80.6	75.5	80.0
ASR	20.2	19.0	19.6	19.2	19.4	19.2	19.7
PSR	16.9	15.4	16.1	14.9	15.4	15.5	17.0
IOW/GL	0.38	0.40	0.39	0.40	0.39	0.40	0.40
MVSW	1.7	1.9	1.9	2.4	2.2	2.0	1.8
STR	4.3	3.9	5.0	1.3	5.0	5.0	5.0
SLW/H	0.99	1.10	1.04	1.04	1.11	1.08	0.92
INR/NR	0.82	0.93	0.93	0.86	0.83	0.83	1.21
ACS/PCS	0.83	0.79	0.80	0.76	0.80	0.78	0.94
TL/TTL	0.26	0.27	0.27	0.26	0.26	0.26	0.24
ED/GL	0.17	0.18	0.19	0.19	0.19	0.19	0.17
Max. teeth	23.6	24.8	25.7	24.5	26.2	25.6	16.9
M/F SVL	0.86	0.91	0.75	0.81	0.78	0.81	0.77
PD/ED	0.45	0.49	0.43	0.47	0.43	0.45	0.60
PFW/AFW	0.83	0.80	0.76	0.75	0.81	0.84	0.75
SL6/SL7	1.29	1.38	1.26	1.23	1.18	1.42	1.47
ML/FL	0.85	0.67	0.67	0.70	0.69	0.65	0.94
FL/PL	0.92	1.02	1.02	0.97	1.09	1.16	0.96
LDL/VL	0.71	0.66	0.65	0.63	0.64	0.56	0.58
PrF/INL	1.08	0.85	1.11	0.98	0.97	1.01	1.20
SL angle	3.4	3.4	3.5	3.7	3.4	3.2	3.7
Ground color	3.2	4.0	4.0	5.0	4.7	4.3	4.6

C and D, and areas B and G (Fischer's Least Significant difference = 0.37 at 71 df).

CORRELATION.— Nineteen characters were initially analyzed by MANOVA (Table 3). Linear measurements (snout-vent length, gape, interocular width, eye diameter) were significantly correlated ($r > 0.608$). Eye diameter was hypothesized to be affected by an aquatic-terrestrial morph shift, plus had the lowest variance, and was retained. Relative tail length was correlated with subcaudal count ($r > 0.571$), and dropped from further analysis in favor of the non-ratio measurement. Relative eye and interocular proportions were dropped from the discriminant function analysis, since the linear components of each were included separately.

DISCRIMINANT FUNCTION ANALYSIS.— The remaining thirteen characters were statistically analyzed for each sex. For males, Wilks' lambda test resulted in F = 6.245, df=78, 551, p>0.0001, among Areas A–G. Univariate F tests showed ten variables to be significant (p<0.05) based on squared multiple correlations, eliminating anterior scale row count, relative internasal length, and relative chin shield length (Table 4). The test of residual roots indicated that only Factors (= discriminant functions)

TABLE 2. Student's t-test results for sexual dimorphism in *Thamnophis atratus* from area D (Santa Cruz Mountains region); data presented are means, standard deviations and sample sizes.

Character	Males	Females	(p)
Snout-Vent length	420.0 ± 4.6 (25)	468.9 ± 7.5 (25)	0.001
Ventrals	158.4 ± 0.5 (25)	152.4 ± 0.6 (25)	0.001
Subcaudals	80.4 ± 0.5 (25)	72.9 ± 0.4 (25)	0.001
Anterior scale rows	19.5 ± 0.1 (25)	19.2 ± 0.1 (25)	n. s
Midbody scale rows	18.4 ± 0.1 (25)	18.5 ± 0.1 (25)	n. s
Posterior scale rows	15.5 ± 0.1 (25)	15.2 ± 0.1 (25)	n. s
Anterior vertebral stripe width	3.6 ± 0.1 (20)	3.5 ± 0.1 (20)	n. s
Midbody vertebral stripe width	2.3 ± 0.0 (20)	2.2 ± 0.0 (20)	n. s
Stripe value	1.7 ± 0.1 (20)	1.7 ± 0.1 (20)	n. s
6th Supralabial width/height	85.9 ± 0.7 (35)	79.1 ± 0.7 (35)	0.001
Internasal length/width	109.2 ± 1.1 (19)	108.3 ± 1.3 (19)	n. s
Internasal-rostral/nasal-rostral	91.0 ± 1.3 (25)	80.5 ± 1.8 (25)	0.001
Anterior/posterior chin shield	79.3 ± 0.9 (19)	78.7 ± 0.8 (19)	n. s
Tail/total length	26.0 ± 0.2 (18)	24.5 ± 0.2 (18)	0.001
Eye diameter/gape length	18.8 ± 0.2 (30)	18.0 ± 0.1 (30)	0.05
Interorbital width/gape length	39.9 ± 0.3 (16)	36.3 ± 0.3 (16)	0.001

1–3 were significant ($p < 0.0001$), with canonical correlations >0.500. For females, Wilks' lambda test also resulted with $p < 0.0001$ (F = 6.407, df = 78, 535). The univariate F-test found 11 variables to be significant ($p < 0.05$), eliminating internasal-rostral contact and relative chin shield length. The test of residual roots indicated that factors 1–4 were significant ($p < 0.01$), with canonical correlations >0.482.

Canonical plots (Fig. 4) indicate the existence of several distinctive population groups for both sexes. Factor 1 of males and Factor 1 of females separate Area D snakes from Area AB and FG snakes. The chief distinguishing character of Area D snakes is the stripe value: 1.4 for Area D and 4.7 for Areas A, B, F, and G. Ventral count is nearly identical for males between Areas D and G, but the Area D mean (153.4) was lower than the mean for Areas A, B, and F (159.2). Posterior scale row counts in Area D are lower than all others: 15.0 vs. 15.6. For Area D, midbody stripe width averages wider (2.7 scale rows) than other Areas (combined average of 2.0 scale rows).

Factor 2 of males and factor 3 of females separate North and South Bay populations, although supporting characters are not discretely different. Area F–G males are longer than Area A–B males (mean snout-vent length = 409.7 mm vs. 392.9 mm), have larger eyes (mean eye diameter = 3.05 mm vs. 2.84 mm), shorter tails (tail length/total length = 0.259 vs. 0.267), fewer subcaudals (mean = 78.8 vs. 83.3), and more pointed internasals (internasal length/width = 0.83 vs. 0.93). Stripe value differs (4.9 for Areas F, G, 4.3 for Areas A, B; t = 10.9 at 225 df, $p < 0.001$), but is thought to be influenced by intergradation with Area D snakes in coastal Marin County snakes. Females have significantly taller 6th supralabials in Areas F–G (supralabial width/height = 0.80 vs. 0.87).

Factor 3 of males and Factor 2 of females separate between Areas A and B and Areas F and G at a significant level ($p < 0.001$), based on ventral count (mean = 148.8 vs. 154.6 for females), midbody stripe width (mean = 1.8 vs. 1.9), and snout-vent length (mean = 394.5 mm vs. 493.9 mm for females). Factor 1 of males also distinguishes Area A from B based on posterior scale row count (mean 15.4 vs. 16.1) and stripe value (mean = 3.9 vs. 5.0).

Predicted vs. actual assignments based on discriminant scores shows homogeneity (at least 75% correct assignment) for all but Areas C and F (Table 5). For Area C, 70.0% of the snakes are correctly assigned, while an additional 13.3% are assigned to Area D and 3.3% to Area A. For Area F, 65.4% of the snakes are correctly assigned, while 15.4% are assigned to Area B and 13.5% are assigned to Area G.

TABLE 3. Summary of basic statistics (mean, standard deviation, range) for male and female *Thamnophis atratus*; abbreviations as in Table 1.

Area	N	SVL	V	SC	ASR	MSR	PSR	G	ED	IOW	AVSW
♂♂											
A	16	380.3 ± 27.5	157.1 ± 4.0	83.8 ± 4.1	19.0 ± 0.0	19.0 ± 0.0	15.4 ± 0.8	14.8 ± 1.1	2.7 ± 0.2	5.9 ± 0.2	3.2 ± 0.6
		(350-430)	(149-164)	(76-93)	(19)	(19)	(15-17)	(13.0-16.8)	(2.2-3.1)	(5.5-6.4)	(2.1-4.3)
B	14	407.4 ± 25.3	161.1 ± 3.8	82.7 ± 3.6	19.6 ± 0.9	19.0 ± 0.0	16.1 ± 1.0	15.8 ± 1.2	3.0 ± 0.2	6.1 ± 0.4	2.9 ± 0.4
		(355-462)	(156-168)	(75-88)	(19-21)	(19)	(15-17)	(13.9-18.7)	(2.6-3.4)	(5.5-7.0)	(1.9-3.3)
C	15	406.7 ± 25.1	150.9 ± 4.0	77.2 ± 4.0	19.3 ± 0.7	18.5 ± 0.9	15.0 ± 0.0	15.9 ± 1.2	2.9 ± 0.2	6.3 ± 0.4	3.7 ± 0.9
		(365-450)	(144-158)	(71-84)	(19-21)	(17-19)	(15)	(13.8-17.8)	(2.5-3.4)	(5.4-6.7)	(2.8-6.4)
D	32	392.7 ± 30.2	153.4 ± 2.9	79.4 ± 5.0	19.2 ± 0.5	18.1 ± 1.0	14.9 ± 0.4	15.6 ± 1.3	2.9 ± 0.2	6.1 ± 0.4	3.8 ± 0.8
		(350-457)	(146-159)	(67-89)	(19-21)	(17-19)	(13-15)	(12.8-16.0)	(2.6-3.5)	(5.5-7.0)	(2.9-6.5)
E	8	412.6 ± 27.6	157.4 ± 3.2	79.0 ± 4.2	19.5 ± 0.9	18.0 ± 1.1	15.0 ± 0.0	16.6 ± 1.1	3.2 ± 0.3	6.5 ± 0.5	3.8 ± 0.8
		(370-452)	(153-162)	(73-88)	(19-21)	(17-19)	(15)	(15.0-18.0)	(2.7-3.6)	(5.6-7.0)	(3.0-5.0)
F	21	415.3 ± 41.7	159.5 ± 4.9	80.6 ± 4.9	19.4 ± 0.8	18.5 ± 0.9	15.4 ± 0.8	16.0 ± 1.2	3.0 ± 0.3	6.2 ± 0.6	3.6 ± 0.6
		(354-514)	(149-168)	(68-89)	(19-21)	(17-19)	(15-17)	(13.9-18.7)	(2.5-3.8)	(5.1-7.2)	(2.8-5.0)
G	12	400.0 ± 32.0	153.3 ± 3.6	75.5 ± 4.6	19.2 ± 0.8	18.8 ± 0.6	15.5 ± 0.9	16.5 ± 1.1	3.1 ± 0.2	6.6 ± 0.4	2.8 ± 0.6
		(350-461)	(\.49-161)	(65-82)	(19-21)	(17-19)	(15-17)	(14.8-18.5)	(2.8-3.4)	(6.1-7.6)	(1.5-3.5)
♀♀											
A	12	394.5 ± 38.6	148.8 ± 3.9	74.7 ± 2.0	19.3 ± 0.8	18.8 ± 0.6	15.8 ± 1.0	16.4 ± 1.5	2.8 ± 0.3	6.2 ± 0.5	3.3 ± 0.7
		(356-479)	(144-156)	(71-78)	(19-21)	(17-19)	(15-17)	(14.8-19.0)	(2.5-3.4)	(5.2-7.1)	(2.2-4.7)
B	10	493.9 ± 75.2	154.6 ± 2.3	76.1 ± 2.2	19.4 ± 0.8	19.0 ± 0.0	16.0 ± 1.1	20.2 ± 3.2	3.5 ± 0.4	7.1 ± 1.0	3.1 ± 0.7
		(385-609)	(152-159)	(74-79)	(19-21)	(19)	(15-17)	(15.2-25.0)	(3.0-4.3)	(5.7-8.5)	(2.1-4.6)
C	15	442.7 ± 41.7	147.1 ± 3.6	70.1 ± 3.1	19.1 ± 0.5	18.3 ± 1.0	15.5 ± 0.9	18.5 ± 1.8	3.1 ± 0.3	6.8 ± 0.5	3.5 ± 0.8
		(366-525)	(141-151)	(65-75)	(19-21)	(17-19)	(15-17)	(15.1-21.5)	(2.6-3.8)	(6.1-7.9)	(2.0-4.6)
D	32	445.9 ± 69.1	147.1 ± 3.3	70.8 ± 3.1	19.2 ± 0.7	18.2 ± 1.0	15.1 ± 0.5	18.1 ± 2.6	3.3 ± 0.4	6.7 ± 0.8	4.1 ± 1.0
		(351-582)	(141-155)	(64-79)	(18-21)	(17-19)	(15-17)	(14.2-23.3)	(2.6-4.2)	(5.1-8.2)	(2.7-6.3)
E	3	485.7 ± 61.9	147.0 ± 1.7	70.3 ± 3.8	21.0 ± 0.0	17.7 ± 1.2	15.0 ± 0.0	18.9 ± 1.7	3.3 ± 0.4	7.3 ± 0.7	3.7 ± 0.6
		(417-537)	(146-149)	(66-73)	(21)	(17-19)	(15)	(16.9-19.9)	(2.9-3.7)	(6.5-7.9)	(3.1-4.2)
F	31	471.5 ± 80.2	154.3 ± 5.34	73.6 ± 4.1	19.5 ± 0.9	18.6 ± 0.8	15.3 ± 0.8	18.7 ± 2.7	3.3 ± 0.4	6.9 ± 0.8	3.5 ± 0.5
		(359-701)	(142-167)	(66-83)	(19-21)	(17-19)	(15-17)	(15.0-24.4)	(2.5-4.1)	(5.5-8.7)	(2.9-4.9)
G	12	463.5 ± 68.7	147.6 ± 4.1	69.8 ± 3.0	19.3 ± 0.8	18.7 ± 0.8	15.8 ± 1.0	19.4 ± 2.3	3.3 ± 0.3	7.4 ± 0.8	3.0 ± 0.4
		(368-627)	(140-156)	(63-74)	(19-21)	(17-19)	(15-17)	(15.8-23.0)	(2.8-3.8)	(6.0-8.5)	(2.3-3.6)

TABLE 3. Summary of basic statistics (mean, standard deviation, range) for male and female *Thamnophis atratus* (continued).

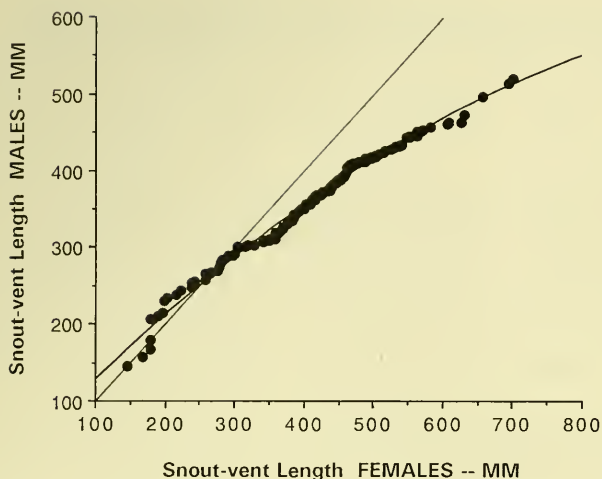| MVSW	STR	R1	R2	R3	R4	R5	R6	R7
1.9 ± 0.5	3.9 ± 1.4	1.10 ± 0.10	0.94 ± 0.21	0.93 ± 0.10	0.79 ± 0.08	0.27 ± 0.01	0.18	0.40
(1.2-2.9)	(1.0-5.0)	(0.94-1.32)	(0.66-1.45)	(0.81-1.16)	(0.66-0.98)	(0.26-0.28)	(0.15-0.21)	(0.36-0.44)
1.9 ± 0.3	5.0 ± 0.0	1.04 ± 0.06	0.93 ± 0.17	0.93 ± 0.07	0.80 ± 0.09	0.27 ± 0.01	0.19	0.39
(1.3-2.6)	(5.0)	(0.93-1.17)	(0.66-1.30)	(0.82-1.07)	(0.66-1.00)	(0.25-0.29)	(0.15-0.20)	(0.35-0.42)
2.5 ± 0.2	2.8 ± 1.2	1.10 ± 0.08	0.95 ± 0.20	0.85 ± 0.10	0.77 ± 0.07	0.27 ± 0.01	0.18	0.39
(2.2-3.0)	(1.0-5.0)	(0.98-1.23)	(0.61-1.31)	(0.68-1.00)	(0.65-0.90)	(0.25-0.29)	(0.17-0.21)	(0.35-0.45)
2.4 ± 0.6	1.3 ± 0.7	1.04 ± 0.09	0.85 ± 0.17	0.86 ± 0.08	0.76 ± 0.08	0.26 ± 0.01	0.19	0.40
(1.6-4.0)	(1.0-4.0)	(0.76-1.24)	(0.45-1.09)	(0.75-1.00)	(0.53-0.96)	(0.22-0.28)	(0.16-0.22)	(0.35-0.45)
2.3 ± 0.2	3.1 ± 1.0	1.09 ± 0.06	0.99 ± 0.10	0.83 ± 0.04	0.81 ± 0.07	0.26 ± 0.01	0.19	0.39
(2.1-2.7)	(1.0-4.5)	(0.98-1.18)	(0.84-1.12)	(0.78-0.89)	(0.71-0.91)	(0.25-0.26)	(0.18-0.20)	(0.36-0.43)
2.2 ± 0.2	5.0 ± 0.0	1.11 ± 0.07	0.92 ± 0.14	0.83 ± 0.07	0.80 ± 0.09	0.26 ± 0.01	0.19	0.39
(1.8-2.5)	(5.0)	(0.99-1.21)	(0.59-1.25)	(0.67-0.96)	(0.56-0.99)	(0.24-0.28)	(0.16-0.22)	(0.33-0.44)
2.0 ± 0.2	5.0 ± 0.1	1.08 ± 0.10	0.92 ± 0.17	0.83 ± 0.08	0.78 ± 0.06	0.26 ± 0.01	0.19	0.40
(1.5-2.4)	(4.5-5.0)	(0.91-1.26)	(0.64-1.26)	(0.62-0.95)	(0.67-0.89)	(0.25-0.27)	(0.17-0.21)	(0.36-0.44)
1.7 ± 0.6	3.8 ± 1.0	0.88 ± 0.11	1.08 ± 0.14	0.83 ± 0.16	0.79 ± 0.08	0.25 ± 0.01	0.17	0.39
(1.2-2.8)	(2.0-5.0)	(0.75-1.20)	(0.91-1.46)	(0.56-1.15)	(0.67-0.95)	(0.24-0.27)	(0.15-0.21)	(0.35-0.42)
2.0 ± 0.4	4.5 ± 0.4	0.86 ± 0.07	1.05 ± 0.09	0.80 ± 0.17	0.76 ± 0.06	0.25 ± 0.01	0.18	0.36
(1.2-2.4)	(4.0-5.0)	(0.72-0.95)	(0.93-1.18)	(0.57-1.08)	(0.66-0.85)	(0.24-0.26)	(0.15-0.20)	(0.32-0.40)
2.4 ± 0.3	2.5 ± 0.8	0.82 ± 0.06	1.13 ± 0.07	0.86 ± 0.14	0.77 ± 0.07	0.24 ± 0.01	0.17	0.39
(2.1-2.9)	(1.5-4.0)	(0.70-0.90)	(0.99-1.25)	(0.66-1.07)	(0.65-0.88)	(0.23-0.26)	(0.15-0.19)	(0.34-0.42)
2.9 ± 0.9	1.4 ± 0.7	0.79 ± 0.09	1.04 ± 0.07	0.83 ± 0.13	0.74 ± 0.07	0.24 ± 0.01	0.18	0.37
(1.8-4.6)	(1.0-3.0)	(0.60-0.97)	(0.88-1.16)	(0.58-1.07)	(0.59-0.88)	(0.22-0.26)	(0.15-0.20)	(0.32-0.42)
2.2 ± 0.4	2.7 ± 1.5	0.79 ± 0.05	1.15 ± 0.11	0.77 ± 0.11	0.77 ± 0.04	0.24 ± 0.01	0.19	0.38
(1.5-2.9)	(1.0-4.0)	(0.74-0.84)	(1.05-1.27)	(0.69-0.90)	(0.73-0.81)	(0.23-0.25)	(0.17-0.22)	(0.38-0.39)
2.2 ± 0.4	4.9 ± 0.3	0.79 ± 0.08	1.05 ± 0.10	0.84 ± 0.18	0.78 ± 0.08	0.24 ± 0.01	0.18	0.37
(1.0-2.8)	(3.0-5.0)	(0.59-0.96)	(0.89-1.27)	(0.49-1.19)	(0.62-1.03)	(0.22-0.27)	(0.15-0.21)	(0.33-0.41)
2.0 ± 0.2	4.9 ± 0.3	0.82 ± 0.08	1.09 ± 0.09	0.85 ± 0.15	0.76 ± 0.06	0.24 ± 0.01	0.17	0.38
(1.6-2.4)	(4.0-5.0)	(0.69-0.98)	(0.94-1.23)	(0.57-1.10)	(0.69-0.84)	(0.22-0.26)	(0.15-0.18)	(0.34-0.42)

FIGURE 3. Relationship of male vs. female snout-vent length for *Thamnophis atratus*. Individual male and female SVL are contrasted in decreasing order of SVL beginning with largest male and female; diagonal line represents a 1:1 ratio.

PHYLOGENY. — The phylogenetic analysis compared areas A, B, D, F and G using *T. a. hydrophilus* (Shasta County populations) as an outgroup. The parsimony analysis resulted in a single shortest tree of length = 103, CI = 0.848 (Fig. 5). Southern populations of *T. atratus* formed two main branches leading to areas A and D, and to a clade containing areas (G (B, F)). Character support and values for branches are provided in Appendix C. The following characters were homoplasious: relative 6th SL height, internasal-rostral contact, relative tail length, posterior/anterior frontal width, ventral width of 6th/7th supralabial, and ground color.

TEST OF CONVERGENCE. — The non-convergence tree (minus *T. e. terrestris*) was best supported (length = 41, CI = 0.800), while the convergence hypothesis tree (minus *T. a. hydrophilus*) obtained only modest support (length = 43, CI = 0.571). The non-convergence phylogeny supported the *T. a. atratus-T. a. hydrophilus* sister-taxa relationship by relative internasal width, pupil diameter and tail length, and male/female snout-vent length. The convergence phylogeny supported a *T. elegans-T. a. atratus* relationship by relative interocular width, stripe value, and ground color. Character convergence between southern *Thamnophis atratus* and *T. elegans* appears to be based only on color pattern, a shorter muzzle and greater relative interocular width as compared to *T. a. hydrophilus*.

DISCUSSION

SEXUAL DIFFERENCES. — Sexual differences in *T. atratus* are based on characters of proportion and ventral-subcaudal counts. Smaller eyes and taller supralabials in females (p<0.001) may be the result of ontogenetic scaling and larger female body size. In large adults, eye diameter increases with respect to gape in males (r = 0.88) and decreases with respect to gape in females (r = -0.93).

Males of the *T. couchii* complex average 82% of female snout-vent length (SVL) (Fitch 1984). Fitch (1981) found the ratio of male-female SVL to increase from aquatic (73%) to terrestrial (88%) *Thamnophis*. In southern *T. atratus*, values are within the range of "terrestrial" snakes (83–96%, mean 89%), as is the value for *T. a. hydrophilus* (87%), while the value for *T. elegans* (77%) approaches the "aquatic" value. The male-female SVL ratio for *T. atratus* appears to be correlated with mean female SVL: (r = 0.91, F = 18.8, p<0.01), but not with male SVL (r = 0.60, F = 2.3, p<0.2). This ratio can be explained by the differential growth rates of adults, in which females continue to increase SVL at a greater rate than males (r = 0.99; Fig. 2). The conflict between these and Fitch's results may be due to a complexity of parameters affecting garter snake size that defy a "terrestrial" and "aquatic" classification scheme.

LENGTH. — Snakes from the coastal fog belt average smaller than those occurring just outside of this zone. Of 20 adult snakes from Dillon Beach, Marin County, only 3 (15%) exceeded the mean SVL for area A. Fox (1951) suggested that the coastal snakes grew less rapidly than inland snakes, causing them to reach maturity at a smaller size. Snakes from near the coast in Areas C and D are also smaller, but less markedly so, than the means for their entire areas.

TABLE 4. Character weights and factor loadings for canonical plots between Areas for male and female *Thamnophis a. stratus*. Only significant values contributing to canonical separation of factors are shown. Abbreviations as in Table 1, except AVSW = anterior vertebral stripe width, INL/INW = internasal length/internasal width, MSR = midbody scale rows.

	Males				Females				
	Weight	F1	F2	F3	Weight	F1	F2	F3	F4
ACS/PCS	n. s.				n. s				
ASR	n. s				0.140				0.675
AVSW	0.247				0.225				
ED	0.258		0.445		0.199		0.408		
INL/INW	n. s				0.121				
INR/NR	0.201		0.427		n. s				
MSR	0.179				0.117				
MVSW	0.241	0.214			0.320	0.199	0.437		
PSR	0.255	0.219			0.138				
SC	0.240		0.408		0.304			0.677	
SLW/H	0.111				0.128			0.309	
STR	0.794	0.838	0.306		0.837	0.770		0.435	
V	0.457	0.286		0.728	0.419	0.235	0.563		

EYE MORPHOLOGY. — Fitch defined his *elegans* group as possessing relatively smaller eyes, larger pupils and darker irises than the *hydrophilus* group. However, neither Bellemin and Stewart (1977) nor Rossman (pers. comm.) found significant differences in eye diameter between *T. elegans* and *T. atratus*, and no significant difference in relative eye diameter was found between southern *T. atratus* populations. Small pupils in highly aquatic *Thamnophis* appear to be an adaptation to increase underwater visual acuity (Schaeffel and de Queiroz 1990). Aquatic *Thamnophis* also possess pale irises, whereas diurnal, terrestrial snakes such as *Coluber, Masticophis*, and *Thamnophis elegans*, possess dark irises (pers. obs.), perhaps to reduce sun glare. Iris color follows a north-south cline towards darker irises in *T. atratus*, and Fox (1951) characterized *T. a. atratus* as having a darker iris than *T. a. aquaticus*. However, southern *T. atratus* retain a pupil size characteristic of highly aquatic snakes.

HEAD SHAPE. — Fitch (1940) characterized the *hydrophilus* group as possessing a relatively pointed muzzle and shorter posterior supralabials than snakes of the *elegans* group, and Fox (1951) found *T. elegans* to possess a shorter gape relative to head length. Within southern *T. atratus*, no identifiable linear clines were found for supralabial height, relative internasal width, or internasal-rostral contact. These snakes retain the relatively short posterior supralabials and pointed internasals of aquatic snakes, but possess a wider snout characteristic of *T. elegans* (Table 1). Southern *T. atratus* also retain the longer gape of the *hydrophilus* group. Gape length is determined by length of supratemporals, quadrates and mandibles (Varkey 1979).

COLOR PATTERN. — The presence of a predominantly spotted pattern in northern *T. atratus* is limited to populations north of the present study area, except near the mouth of the Russian River, based on examination of MVZ and CAS specimens. Thus, all snakes utilized here are relatively dark with bright stripes. Variation in stripe value converges on Area D: as the Santa Cruz Mtns. are approached, vertebral stripe width and ventral darkening increase, and lateral stripe contrast decreases (Fig. 1f). Parallels to this pattern occur in the Puget Sound region of Washington, where the three species of *Thamnophis* occurring there exhibit increased melanism (Stebbins 1985), which is the diagnostic character for two subspecies: *T. elegans nigrescens* and *T. sirtalis pickeringii*. Two *T. atratus* from coastal Sonoma County (MVZ 48013 and 48016) show ventral and lateral melanism,
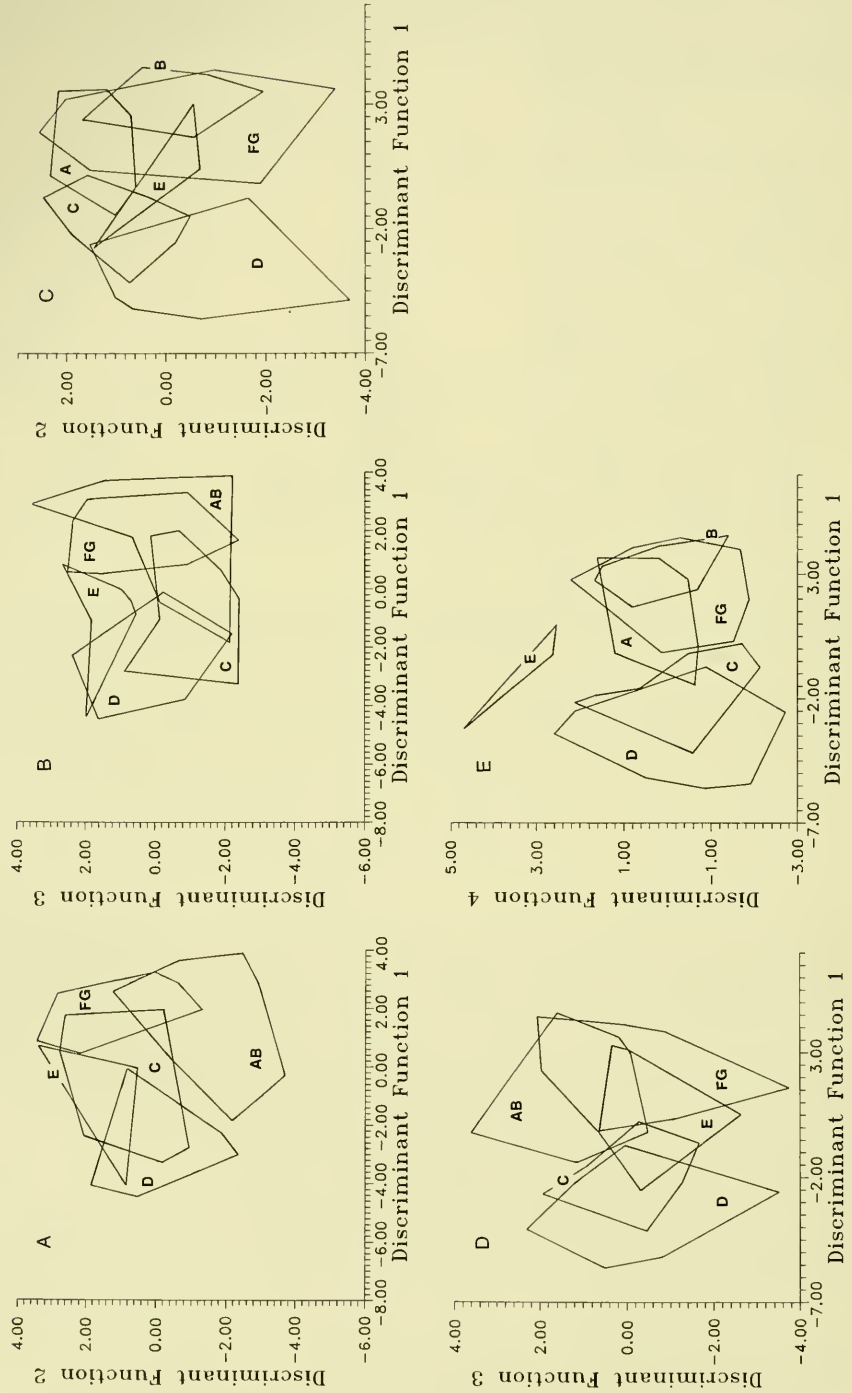
FIGURE 4. Canonical plots for discriminant functions for male (A, B) and female (C–E) *Thamnophis atratus*; polygons enclose minimum area based on outermost individual snakes; letters within polygons refer to Areas A–G.

TABLE 5. Predicted vs. actual results of group membership in a discriminant function analysis of *Thamnophis atratus* from Areas A-G.

Area	A	B	C	D	E	F	G	Total	
A	21	2	3			2		28	A
B		20				4		24	C
C			21	4	2		2	30	T
D			7	57				64	U
E				1	10			11	A
F	2	8			1	34	7	52	L
G						3	21	24	
Total	23	30	31	62	13	43	30		

PREDICTED

although the narrow vertebral stripe and cephalic proportions in these specimens are indicative of *T. a. hydrophilus*. Other snakes from this area possess a paler, three-striped pattern.

Fox (1951) found Area A–B snakes to have a gray ground color, pale yellow vertebral stripe, and salmon midventral suffusion (Fig. 1d). Area D–G snakes have abundant black suffusion on the dark fields, a bright yellow to yellow-orange vertebral stripe, and yellow or yellow-orange midventral suffusion (Fig. 1f–h). The latter two characters fade in preservative and were not quantified for the present study. Area F snakes show an overall increase in the amount of yellow in the pattern, paralleling another Diablo Range endemic, *Masticophis lateralis euryxanthus* (Riemer 1954), and *Thamnophis sirtalis fitchi* in the southern Diablo and Santa Lucia ranges (pers. obs.).

CANONICAL SEPARATION AND PHYLOGENETIC IMPLICATIONS. — Specimens from Area D were the most significantly differentiated from other Areas (mean Chi-square = 375.6; Factor 1). Area D snakes possess a unique color pattern, which all young of several broods from this Area displayed. The light, three-striped pattern is omnipresent in all broods examined from Areas A, B, and F, and in broods from Areas C and E the patterns are mixed. Because of their unique color pattern, combination of other character extremes, and phylogenetic position, restriction of the name *Thamnophis a. atratus* to Area D is warranted (see Taxonomic Synopsis).

Despite the numerous characters that distinguish between populations north and south of San Francisco Bay, the branching pattern of the phylogenetic tree indicates that Areas A and B are divergent. This is supported by Factor 3 for males and Factor 2 for females, which separate Areas A from B and Areas F from G. Thus, *T. a. aquaticus* is polyphyletic.

The branching pattern of the phylogenetic tree indicates divergence between (A, D) and ((B, F) G). Factor 3 of males and Factor 2 of females reflect this pattern, while factor 2 of males and factor 3 of females reflects Fox's (1951) arrangement of *T. a. atratus* and *T. a. aquaticus*. Because Area A and B snakes are geographically proximal to the outgroup (ancestral taxon), they hypothetically represent basal populations to the clades formed by node 2, and are not as readily distinguishable from each other as the more geographically distant populations (D and F,G). The phylogenetic tree can alternately be viewed as containing 2 ([A, D] and [B, F, G]) or 3 (A, D, and [B,F, G]) terminal taxa. The latter alternative would require recognition of *T. a. aquaticus* in Area A, creating an intermediate taxon that would be difficult to diagnose. The two-taxon alternative corresponds to a bifurcation of coastal and inland populations near the southern end of the range of *T. a. hydrophilus*. This latter alternative is utilized here to avoid taxonomic recognition for populations that would be based on intermediate characters within a north-south cline.

Populations composing both clades have evidently diverged on separate trajectories from *T. a. hydrophilus*. The coastal clade includes *T. a. atratus* in the restricted sense, while the inland clade
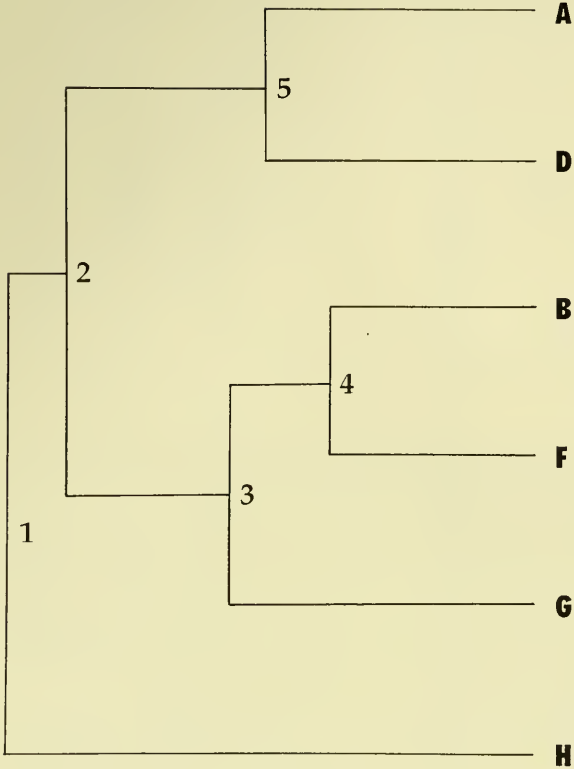
FIGURE 5. Phylogenetic relationships of five population groups of *Thamnophis atratus* (Areas A, B, D, F, G) using *T. a. hydrophilus* (H) as the outgroup; length = 103, CI = 0.848; numbers identify nodes referred to in the text.

represents a distinct taxon described below. The populations in areas A and B, formerly called *T. a. aquaticus*, are here referred to as "basal-southern" *T. atratus*.

INTERGRADES. — Within the range of southern *T. atratus* are several areas of morphological intergradation. Areas A and C are composed of snakes intermediate in color and pattern between the subspecies *T. a. hydrophilus* and *T. a. atratus* (Fig. 1e). The change is gradual from the Marin Peninsula to the San Andreas Rift Lakes (Fig. 6), although some snakes from Half Moon Bay to Pescadero have faint lateral stripes. This appears to be clinal intergradation, in which characters have shifted along a geographic gradient from one extreme to another. The ends of these extremes are homogeneous (at least morphologically) groups of populations. Snakes from northwestern Sonoma County have high ventral counts, occasionally lack lateral stripes, and may have dark spots in the dark fields. Although *T. a. hydrophilus* may be striped and/or spotted, the spotted pattern is unique to that subspecies, and is seen in snakes as far south as the Gualala River on the coast and Cache Creek, Colusa County, inland. Fox (1951) considered intergradation between the subspecies *T. a. hydrophilus* and "*T. a. aquaticus*" to be abrupt, both morphologically and geographically, ocurring at the Gualala River.

Fox (1951) stated, "the transition from *aquaticus* to *atratus* [striped morph] is gradual, . . . I have arbitrarily divided the two races at the San Francisco Bay." Fox's concept of the subspecies *T. a. aquaticus* included the variable populations ranging north to Trinity County. He cited the four Solano County specimens as being intergrades because of enlarged supralabials and intermediate color. The large size of the supralabials is due to the fact that two are huge females (with enlarged salivary glands). One male has supralabials in proportion with other Area B snakes, and those of the other could not be measured. All have the gray ground color typical of "*T. a. aquaticus*" but vertebral stripes similar to the striped morph of *T. a. atratus*. Snakes from Contra Costa County are typical of the striped form of *T. a. atratus*. Unfortunately the subtle color differences between "*T. a. aquaticus*" and striped *T. a. atratus* are not evident in preserved specimens, and no fresh specimens from Contra Costa County were available for study. MVZ 48975, from Wildcat Canyon, Contra Costa County, has a gray dorsum with a narrow vertebral stripe as in *T. a. aquaticus*. However, two others collected with this individual lack these characteristics (pers. obs.). No snakes were available from the Carquinez Straits region between Suisun Creek and the Berkeley Hills. The southernmost area of intergradation between *T. a. hydrophilus* and southern *T. atratus* remains unresolved as to whether it is abrupt or gradual. A genetic study is needed to determine the nature of contact at points of parapatry.

Area E contains a mixture of snakes bearing character extremes, and others which are intermediate. The dark form of *T. a. atratus* occurs south to Uvas Canyon, while striped snakes overlap the dark form north to the Los Gatos Creek drainage (Fig. 6). At Uvas Canyon and upper Guadalupe Creek, both morphs and intergrades occur sympatrically. Of 26 snakes from Area E and Guadalupe Creek, 38% are dark, 19% are striped, and 43% are intermediate. All snakes in the open oak woodland below Uvas Canyon and south of the Santa Teresa Hills are the striped morph, and are identical in color pattern to snakes east of the Santa Clara Valley. This distribution of color morphs and intermediates suggests secondary contact in Area E (see Biogeography below).

The southwestern side of the Santa Cruz Mountains, from Soquel Creek east, contains populations of intergrade snakes having faint lateral stripes and slightly darkened venters (Fig. 1g). It is possible that these snakes resulted from initial contact when the striped form reached the south end of the Santa Cruz Mountains (see below). The intergrade zone may have broadened, creating a buffer from constant influence from the striped form. Also, the heavily forested summit may prevent the striped form from remaining in contact with most of these populations. There is some gradation, with snakes from the geographical extremes (Soquel Creek and Hecker Pass) increasingly resembling the dark and striped forms, respectively.

ECOLOGY. — At the northern end of the range of *Thamnophis atratus*, the subspecies *T. a. hydrophilus* is highly aquatic (Fitch 1940), while snakes from the San Francisco Bay region are semiterrestrial (Fox 1951, pers. obs.). This ecological shift is thought to be the result of change in habitat and, possibly, competition with other species of *Thamnophis*.

Southwestern Oregon and northern California have an abundance of large rivers, and large museum series of *T. atratus* collected on single dates along these rivers indicate their abundance there. The rivers are typically lotic all year, with rock, sand, or gravel beds, and snakes rarely venture far from these or smaller bodies of water (Fitch 1940). There are few large rivers or streams in the San Francisco Bay region and most are intermittent. Here, *T. atratus* has adapted to a semiterrestrial life style, and acquired some morphological characteristics of Fitch's (1940) *elegans* group. South of the Pajaro River drainage large rivers are again prevalent and, except on the outer coast, *T. atratus* has retained an aquatic life style (S. Sweet, pers. comm.). The morphological differences between southern *T. atratus* and *T. a. hydrophilus* may be related to these differences in habitat.

Much of the range of *T. a. hydrophilus* (southwestern Oregon and northern California) is forested. Southward and inland, canopy vegetation is patchy in oak savannah-woodland, and is often restricted to riparian strips. This is reflected in an increased coastward restriction of *T. atratus* distribution from north to south. In conjunction, the drab, spotted morph of *T. a. hydrophilus* has been lost in southern *T. atratus*. The drab, spotted pattern provides a camouflage advantage in open, gravel-bottomed streams (Fitch 1940). Snakes moving on the bottom of these streams are nearly invisible, and I have lost sight of snakes, even though in plain view, as their pattern and sinuous movements blended with the gravel and riffles. A boldly striped pattern might be detrimental to survival in such situations. *Thamnophis atratus* in Coyote Creek were readily observed at distances >10 m due to their contrasting pattern and bright colors. However, striping is advantageous to terrestrial snakes as both camouflage in vegetation, and as an illusionary escape device. The dorsal stripe leaves the observer with a brief after-image posterior to the retreating snake (Jackson et al. 1976), and I have found this to be effective when trying to capture rapidly crawling snakes on land. Striping in snakes, possibly detrimental in the water, may be offset by its terrestrial advantage, since seasonal drying of streams forces the snakes to terrestriality during part of the active season. I believe that selection for a boldly striped pattern in southern *T. atratus* has positive survival value, and is related to the marked habitat differences between northern and central California. However, *T. a. hydrophilus* exhibits an increase in number of striped individuals inland, but does not show seasonal disuse of streams during the annual period of activity (D. Rossman, pers. comm.).
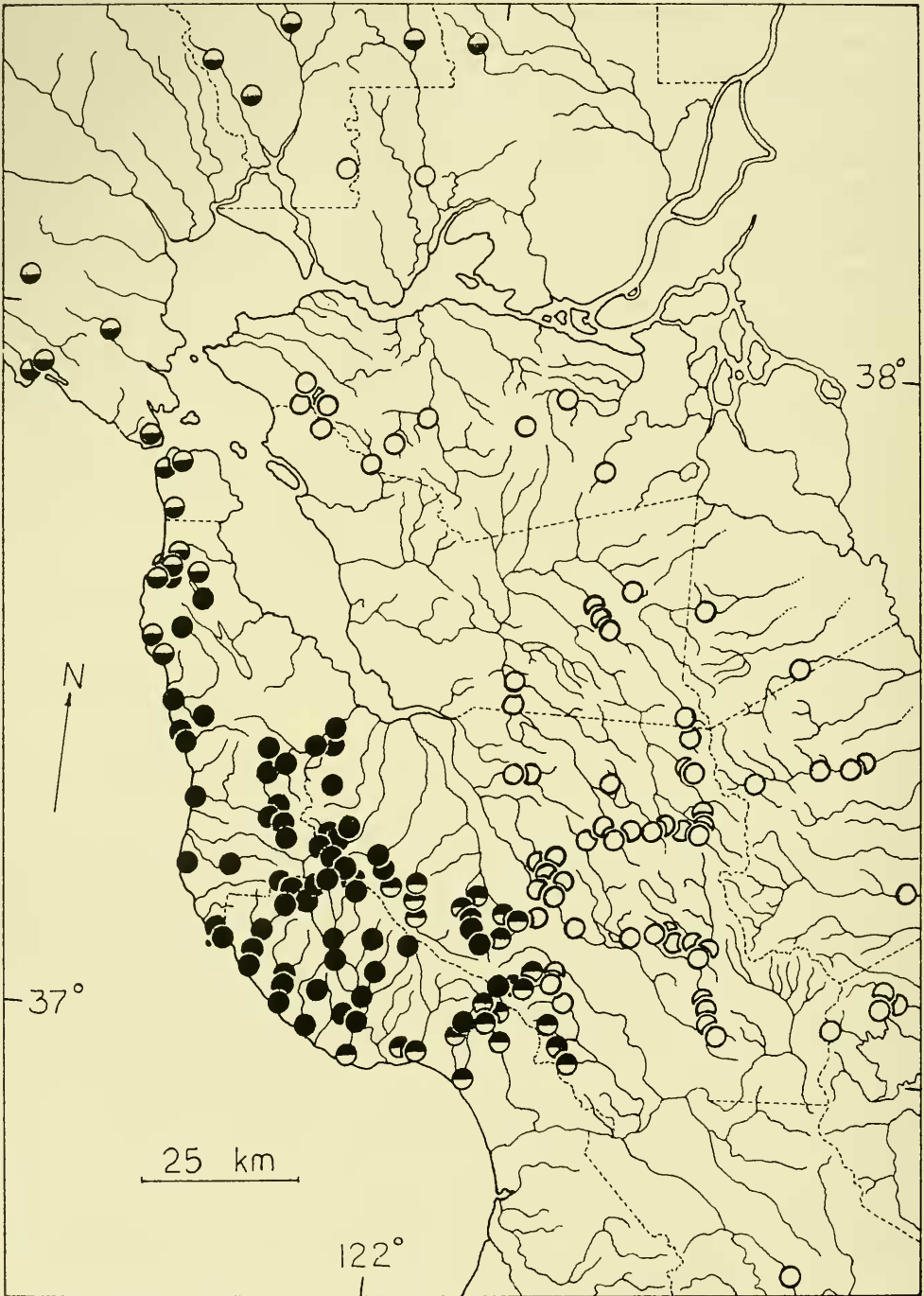
FIGURE 6. Localities for *Thamnophis atratus* in the San Francisco Bay region. Circles darkened below represent basal southern *T. atratus*; open circles, *T. a. zaxanthus*; closed circles, *T. a. atratus*; circles darkened above, *T. a. atratus* × *T. a. zaxanthus* intergrades.

Within Area D, both prey and understory vegetation are widely dispersed. In Area F, prey and cover are restricted to riparian strips, which is reflected in habitat use by snakes: 52.5% (G = 0.718) of Area D snakes were encountered within 20 m of water, compared to 88.2% (G = 10.352) of Area F snakes. Increased cover and prey dispersal has enabled Area D snakes, and probably coastal Area G snakes, to increase terrestriality over other *T. atratus*. Area D snakes are less seasonally restricted in activity, with 61.6% of snakes observed May-August, vs. 73.2% in Area F. May–August activity is significantly greater than spring and fall activity in Area F snakes (t = 2.447 at df = 6, p<0.05), but not for Area D snakes. Snakes from the southern extreme of the range are active from April to July only (S. Sweet, pers. comm.).

FOOD. — Quantitative feeding studies for southern *T. atratus* are unavailable, and Fitch's (1940, 1941) concept of *T. atratus* included *T. elegans terrestris*. For the present study, *T. atratus* were not routinely checked for prey. Observations revealed only fish and amphibians, and feeding was observed only in the water. The presence of the plethodontid salamanders *Aneides lugubris, Batrachoseps attenuatus*, and *Ensatina eschscholtzii* in four snakes from Area D indicates some terrestrial feeding (pers. obs.). Otherwise, there is no indication of similarity with the food habits of *T. elegans* (Fox 1952; Gregory et al. 1980; James et al. 1983).

BIOGEOGRAPHY. — Geographic patterns of variation within the *Thamnophis couchii* complex, combined with paleogeographic and molecular data, suggest the following hypotheses for observed variation within *T. atratus*. *Thamnophis atratus* occasionally hybridizes with sympatric members of the *T. couchii* complex at either end of its range (Rossman and Stewart 1987), but is non-convergent in most characters with *T. couchii* and *T. hammondii* at their respective contact zones. The ranges of *T. atratus* and *T. hammondii* overlap broadly, and hybridization may be the result of secondary contact (S. Sweet, pers. comm.), suggesting that derivation of one from the other is unlikely. The ranges of *T. atratus* and *T. couchii* are largely parapatric, creating a narrow zone of hybridization, which implies derivation of one species from the other. In addition, paleogeographical evidence supports the notion that *T. atratus* originated in the north, and dispersed southward. Scenarios in Peabody and Savage (1958), Howard (1962), Morafka and Banta (1972), and Yanev (1980), indicate that territory currently occupied by southern *T. atratus* was submerged until 5 million years ago (mya). A southward dispersal route for *T. atratus* was supplied by continuing uplift of the Coast Ranges during the next 4 million years.

A scenario for the derivation of morphotypes of *T. atratus* can be developed by superimposing their hypothetical past distribution on maps provided in Yanev (1980). Between 8 and 5 mya the northern Coast Ranges uplifted southward from the present-day vicinity of Lake County, forming a peninsula toward the present-day Santa Cruz Mountains. The interface created by this uplift runs from near the mouth of the Gualala River eastward in the region in which Lake County borders Sonoma and Napa counties. The Sonoma Gap, represented by a low grassland region interrupting the otherwise continuous band of coastal forest, runs east-west approximately 60 km to the south of this interface. A number of taxa have differentiated genetically and/or morphologically near the interface: *Dicamptodon* (Good 1989), *Aneides lugubris* (Sessions and Kezer 1987), *Ensatina* (Stebbins 1949; Wake 1997), *Rana aurora* (Green 1985), *Diadophis amabilis* (Blanchard 1942), and *Thamnophis atratus* (Fox 1951). During this period, it is conceivable that *T. atratus*, or its ancestor, moved southward along the peninsula.

Subsequent uplift and contact with the Diablo Range in the north formed two peninsulas, one extending southward through the Santa Cruz Mountains, the other southward to the vicinity of present-day Pacheco Pass in the Diablo Range. Once *T. atratus* moved south of the Sonoma Gap, two morphotypes may have diverged in response to habitat differences between inner and outer coast. Dark-sided snakes of the outer-coastal forests would have extended southward through the Santa Cruz Mountains, while the three-striped inland morph would have extended southward in the Diablo Range in savannah-riparian strip habitat (Fig. 7a). This scenario is supported by node 2 and the resulting

branches of the phylogenetic tree (Fig. 5). This pattern is paralleled by *Ensatina*, in which an inner-outer coast divergence occurs immediately north of San Francisco Bay, following through to the Santa Cruz Mountains-Diablo Range (Stebbins 1949).

As the Pajaro outlet for the Merced Sea closed about 1 mya, the inland morph may have extended southward through the Santa Lucia Range to the Transverse Ranges south of the Monterey Peninsula (Fig. 8). *Thamnophis atratus* is relatively common on the outer coast, but is scarce inland. This may be due to competition with the highly aquatic *T. hammondii*, perhaps already established in the region, by increased restriction of riparian habitats, and seasonality of water and food supplies. Initial closure of the sea at the Diablo Range would have permitted the inland morph to enter these areas in advance of the Santa Cruz Mountains morph. Subsequent elimination of contact between inner and outer Coast Range populations by the Salinas Valley would explain node 3 of Fig. 5. The eventual shift of the Central Valley outlet to the San Francisco Bay coincides with nodes 4 and 5 of Fig. 5.

Closure of the Santa Cruz-Diablo Range division at the Santa Clara Valley-San Francisco Bay would have allowed secondary contact between populations already differentiated (Fig. 7b). The two morphotypes meet along the southeast slope of the Santa Cruz Mountains, where both intergradation and sympatry occur. Other taxa following a similar pattern include the scorpion *Uroctonus mordax* (Hjelle 1972) and *Lampropeltis zonata* (pers. obs.). By presence-absence, *Pinus sabiniana* also demonstrates this pattern (R. Myatt, pers. comm.). The preceding are woodland species, none of which currently occur at the proposed Santa Clara Valley crossing, suggesting that such a crossover would have taken place during more mesic conditions.

TAXONOMIC SYNOPSIS

Thamnophis atratus zaxanthus subsp. nov.
Fig. 1h

HOLOTYPE. — MVZ 207940, an adult female from 3 mi S of Gilroy Hot Springs, Santa Clara County, California, collected 15 April 1986 by William P. Hutchins.

DIAGNOSIS. — Maximum total length 902 mm; ventrals, males 148–168 (mean 158.3, n = 71), females 140–167 (mean 152.1, n = 86); subcaudals, males 65–89 (mean 80.8, n = 61), females 59–83 (mean 72.5, n = 73); anterior scale rows 19 (82%) or 21 (18%); midbody scale rows 19 (85%) or 17 (15%); posterior scale rows 15 (78%) or 17 (22%); vertebral stripe relatively broad, averaging 3.2 (range 1.5–5.0) scale rows on the nape, 2.1 (1.0–2.8) rows in the thoracic region; vertebral stripe yellow to orange-yellow; lateral stripe conspicuous, pale green; dorsum dark gray to black; iris gray or brown; top of head dark, olive black, with a prominent parietal spot; supralabial suture marks narrow when present; demarcation between dorsal head color and pale supralabials distinct; chin cream, becoming bright yellow on the throat, grading to pale green in the thoracic region; ventral color darkening slightly posteriorly; midventral suffusion yellow to orange; dark markings absent from transverse ventral sutures; eye moderate in size (eye diameter/gape length 0.15–0.22, mean = 0.19 in males, 0.18 in females); tail moderately long, averaging 26.2% (24–29%) of total length in males, 24.4% (22–27%) of total length in females. Color photographs of adults are provided by Boundy (1990, frontispiece, holotype in life), Mara (1994:4, mislabeled *T. sirtalis fitchi*) and Rossman et al. (1996, pl. 1).

DESCRIPTION OF HOLOTYPE. — (from life): Adult female, 448 mm SVL, 128+ mm tail length (approx. 7 mm missing from tip); ventrals 149, subcaudals 62+; scale rows 19-19-15, all but first row keeled; supralabials 8-8; infralabials 9-9 (5th and 6th fused on each side); preoculars 1-1; postoculars 3-3; temporals 1+2+2 on each side; posterior chin shields longest; intergenials 3; anal plate single; head distinctly wider than neck; top of head flat; snout moderately blunt; eyes and nostrils with a slight dorsolateral tilt; pupil approximately 1/2 eye diameter; iris dark gray; eye diameter/gape length
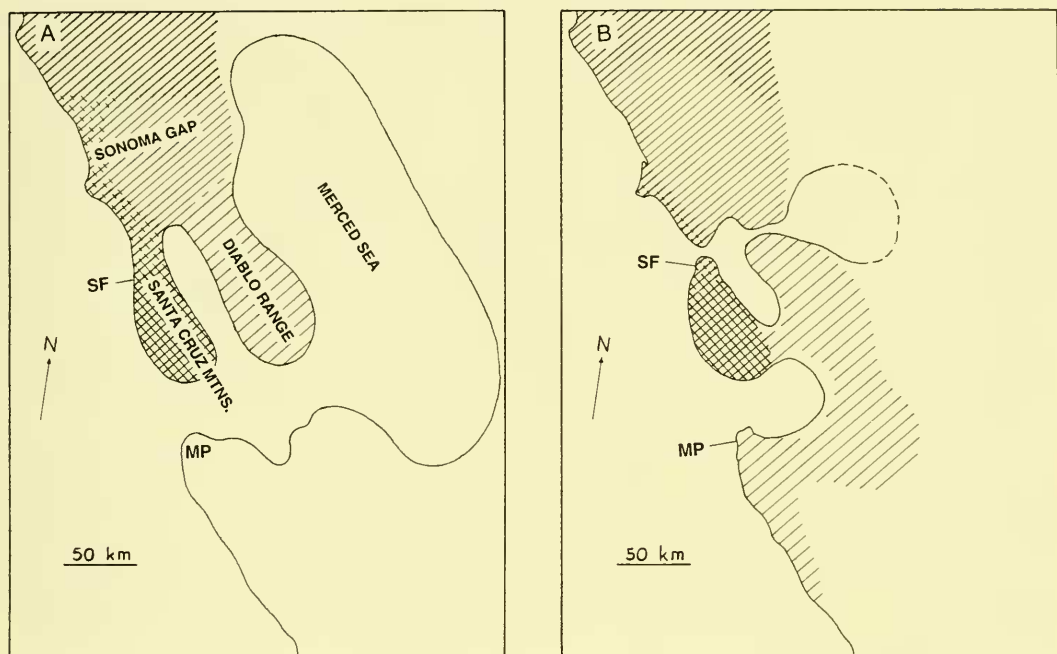
FIGURE 7 (A) Hypothetical distribution of southern *Thamnophis atratus* 1 million years ago; crosshatching represents *T. a. atratus*; area of widely spaced lines represents *T. a. zaxanthus*; SF = present day location of San Francisco; MP = Monterey Peninsula. (B) Hypothetical distribution of *T. atratus* 0.5 million years ago.

0.17; top of head dark olive gray, becoming lighter at preoculars; parietal spot present; labials and side of neck to about one head-length posterior of jaw angle bright yellow, slightly lighter yellow on ventrals to about two head-lengths posterior of throat; chin yellow cream; narrow black sutures present between all but first two supralabials; upper half of supralabials dusky yellow; venter pale gray green, gradually becoming darker posteriorly, with midventral yellow suffusion; olive-gray ventrolateral stripe on first scale row and tips of ventrals, beginning at the 11th ventral; small black markings on anterior edges of first 3 dorsal scale rows; lateral stripe on 2nd and 3rd dorsal scale rows, light olive gray on yellow, the yellow fading posteriorly; vertebral stripe orange yellow, 3 plus two half scale rows wide at nape, narrowing to 1 and two 1/2 rows posteriorly; stripe becoming duller, two half rows wide, on tail to tip; ground color dark olive brown, heavily suffused with black, giving an overall black appearance (Fig. 1h).

VARIATION. — Juveniles are identical in coloration to adults, although they often have brighter, more distinct markings. Intrapopulation variation is limited to shade and intensity of stripe color. Vertebral stripes may be pale yellow to yellow orange. Lateral stripes have varying amounts of olive gray overlaying the yellow, creating a range of pale gray-yellow to bright yellow stripes. Midventral suffusion is yellow, orange or pale salmon.

Interpopulation variation between Diablo Range and Santa Lucia Range snakes consists of the latter having lower ventral and subcaudal counts, a narrower vertebral stripe, and fewer individuals with 20 or 21 anterior scale rows. Diablo Range snakes differ from Napa and Solano county snakes in having a broader vertebral stripe, lower posterior scale row and subcaudal counts, and taller subralabials. Intergrades with *T. a. atratus* exhibit loss of the lateral stripes to a varying degree, with increased dark olive coloration on supralabials, lower sides, and venter (Fig. 1e).

DIAGNOSTIC COMPARISONS. — *Thamnophis a. zaxanthus* differs from other central California *Thamnophis* as follows: from *T. sirtalis* it differs in having 8 rather than 7 supralabials, in lacking a red head and red in the dark fields, and in having a yellow or orange midventral suffusion; from *T. elegans* it differs by always lacking red pigment, and by having a yellow midventral suffusion, the posterior chin shields noticeably longer than the anterior, narrower contact between the internasals and the rostral, the internasals usually longer than wide, the anterior scale rows more often 19 than 21, the posterior scale rows more often 15 than 17, and a smaller pupil relative to eye diameter (Bellemin and Stewart 1977 provide a statistical analysis of these differences); from *T. gigas* and northern populations of *T. atratus hydrophilus* it differs by usually having 19 (80%) rather than 21 or more anterior scale rows, an orange midventral suffusion, bright yellow supralabials and throat, and a vertebral stripe 2 or more scale rows wide. *Thamnophis a. zaxanthus* also differs from *T. a. hydrophilus* in lacking dark markings on the transverse ventral edges, in always lacking distinct dark spots on the dorsum, and in having a darker iris; and from *T. a. atratus* by having lateral stripes, a strong demarcation between the dorsal head and pale supralabial color, and a lighter venter.

ETYMOLOGY. — Greek, *za* (intensive), and *xanthus* (yellow).

DISTRIBUTION. — Inner Coast Range from Napa and Solano to Santa Barbara counties, and the Santa Lucia Range (Fig. 6). It occurs from hills south of the Carquinez Straits to Tres Pinos Creek in the Diablo Range, and to the Pinnacles region in the Gabilan Mountains. It occurs on the coastal slope of the Santa Lucia Range from the Monterey Peninsula south to the San Rafael Mountains, Santa Barbara County (La Brea Creek and Birabent Canyon; S. Sweet, pers. comm.). It also occurs in the foothills along the southeastern slope of the Santa Cruz Mountains, south of the Santa Teresa Hills. It is absent from major valleys.

Thamnophis atratus atratus (Kennicott 1860)
Fig. 1f

LECTOTYPE. — USNM 970a, designated by Fitch (1940:89), from San Francisco (Cochran 1961:181). Descriptions of the cotypes in Kennicott (1860:296) and Cope (1891:658), and examination of lectotype, allow correction of the type locality to Area D, that is, the Santa Cruz Mountains or southern San Francisco Peninsula. The lectotype is an adult male (486 mm SVL) with the following characters: tail/total length 0.260; supralabials 8-8; infralabials 10-10; oculars 1-3/1-3; temporals 1+1+2, 1+2+2; scale rows 19-19-15; pupil/eye diameter 0.30; eye diameter/gape length 0.19; interorbital width/gape length 0.38; posterior/anterior frontal width 0.76; frontal/parietal length 0.89; muzzle/frontal length 0.73; internasal length/width 0.43; prefrontal/internasal length 0.79; internasal-rostral/nasal-rostral 0.80; loreal dorsal/ventral length 0.80; 6th/7th SL angle 3.5; anterior/posterior chin shield length 0.92; vertebral stripe width 2.9; coloration is typical of Area D snakes.

DIAGNOSIS. — Maximum total length 1016 mm; ventrals, males 146–165 (mean 154.2, n = 57), females 141–155 (mean 147.0, n = 57); subcaudals, males 67–89 (mean 79.4, n = 49), females 64–79 (mean 70.3, n = 48); anterior scale rows 19, rarely 17 or 21; midbody scale rows 19 (65%) or 17 (35%); posterior scale rows 15, rarely 13 or 17; vertebral stripe yellow to orange yellow, and broad, averaging 4.0 (range 2.7–6.5) scale rows in the nuchal area, 2.5 (1.6–4.6) rows in the thoracic region; lateral stripes absent; dorsum olive black, grading to dark olive at the ventrals; dorsal black spots obscure; iris dark brown; top of head dark olive brown to olive black, with a prominent parietal spot; supralabial suture marks narrow when present; demarcation between dorsal head color and dusky olive supralabials indistinct; chin cream, becoming deep yellow on the throat; venter abruptly becoming olive gray in the thoracic area, continuously darkening posteriorly; prominent yellow-orange midventral suffusion; dark markings absent from transverse ventral sutures; eye moderate in diameter (eye diameter/gape length 0.15–0.22, mean = 0.19 in males, 0.18 in females); tail moderately
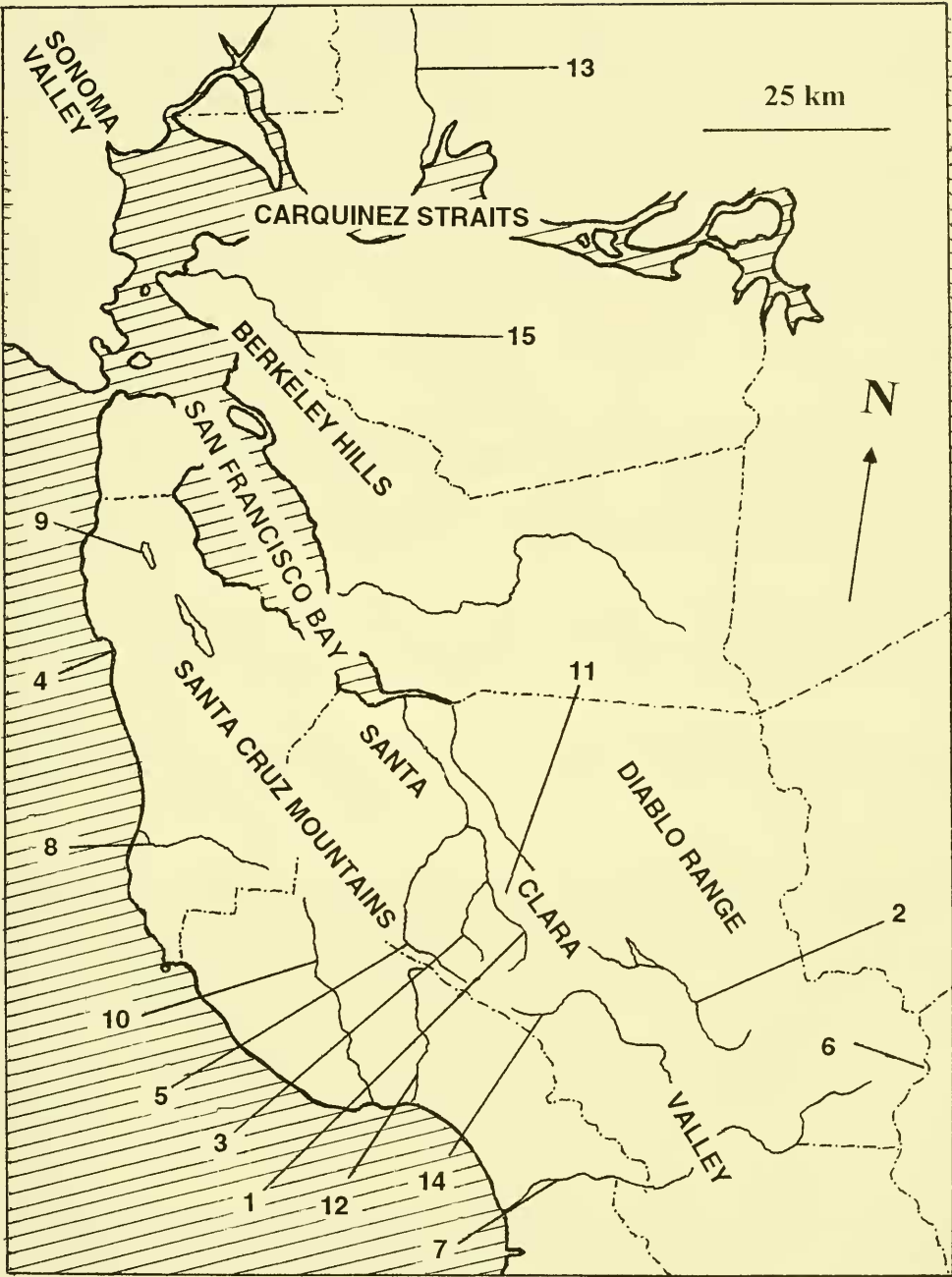
FIGURE 8. Location of localities and geographic features mentioned in the text: 1) Alamitos Creek; 2) Coyote Creek; 3) Guadalupe Creek; 4) Half Moon Bay; 5) Los Gatos Creek; 6) Pacheco Pass; 7) Pajaro River; 8) Pescadero Creek; 9) San Andreas Lake; 10) San Lorenzo River; 11) Santa Teresa Hills; 12) Soquel Creek; 13) Suisun Creek; 14) Uvas Creek; 15) Wildcat Canyon.

long, 26.2% (0.22–0.28%) of total length in males, 24.1% (0.22–0.26%) of total length in females. Color photographs of adults are provided by Mara (1994:13) and Rossman et al. (1996, pl. 1).

DISTRIBUTION. — Santa Cruz Mountains and southern San Francisco Peninsula, from the San Andreas rift lakes to the San Lorenzo River watershed and Uvas Canyon (Fig. 6).

Thamnophis atratus hydrophilus Fitch 1936
Fig. 1a–c

HOLOTYPE. — MVZ 18127, from Trail Creek, 6 mi from its mouth, Jackson County, Oregon.

DIAGNOSIS. — Maximum total length 916 mm; ventrals, males 151–171 (mean 163.6, n = 77), females 148–168 (mean 159.0, n = 71); subcaudals, males 77–95 (mean 87.5, n = 62), females 65–82 (mean 76.3, n = 60); anterior scale rows 21 (73%; northern Humboldt County northward) or 19 (98%; southern Humboldt County southward); midbody scale rows 19 (84%) or 21 (16%); posterior scale rows 17 (46%) or 15 (54%); vertebral stripe narrow, less than 1 and two half scale rows wide, occasionally absent; vertebral stripe cream to orange yellow; lateral stripes absent to prominent; dorsum olive gray to dark olive, with alternating darks spots distinct except in individuals having dark ground color; top of head olive to dark brown, with a distinct parietal spot; paired, dark neck blotches often distinct; supralabial suture marks present, of variable width; demarcation between dorsal head and pale or dusky supralabial color distinct to only slightly so; venter light dusky, with a pale midventral orange to yellow wash; dark markings present on transverse ventral sutures; eye diameter moderate (eye diameter/gape length 0.16–0.22, mean = 0.19 in males and females); tail relatively long, 26.8% (24.1–28.2%) of total length in males, 25.0% (22.6–26.8%) of total length in females. Color illustrations of adults are provided by Smith and Brodie (1982:151) and Rossman et al. (1996, pl. 1).

DISTRIBUTION. — Northern Coast Ranges of California and southwestern Oregon north of the Gualala River and Lake County, California.

SUMMARY

Southern populations of *Thamnophis atratus* are well-differentiated from northern populations (= *T. a. hydrophilus*), and differences appear abruptly along a zone running from near the mouth of the Gualala River eastward to the ridge separating Lake and Napa counties. The southern populations, formerly thought to be separable into subspecies north and south of San Francisco Bay, are found instead to have differentiated on two north-south trajectories (coastal and inland). Populations of *T. atratus* immediately north of San Francisco Bay exhibit little differentiation between coastal and inland populations, but there is increasing divergence in characters between coastal and inland populations south of the Bay. Populations south of the Bay appear to have come into secondary contact at the southeastern part of the Santa Cruz Mountains, where phenotypic hybridization occurs. Elsewhere, the two morphotypes are geographically separated.

The phylogenetic tree produced by the present study, coupled with hypothetical Pleistocene geography of the central California coast, recommends a revised taxonomic arrangement of southern *T. atratus* populations. The north Bay populations, formerly called *T. a. aquaticus*, are morphologically and phylogenetically basal to south Bay populations. Because they lack morphological and phylogenetic uniqueness, they cannot be considered terminal taxa and are not taxonomically recognizaeable. The south Bay populations have evolved on two separate trajectories from north Bay populations. Populations comprising the two trajectories are morphologically and phylogenetically unique, and are therefore given taxonomic status. The coastal trajectory represents *Thamnophis atratus atratus* in a restricted sense, while the inland trajectory is named *T. a. zaxanthus*.

APPENDIX A

Specimens examined for MANOVA (all California).—*Thamnophis atratus aquaticus* (132). Marin Co.: MVZ 18196, 18198, 36184, 40708, 47953, 47957–47966, 47969–47995, 48196 (holotype of *Thamnophis elegans aquaticus*), 172251, 206938. Sonoma Co.: CAS 27939, 28019–28021, 28024, 28025, 28029, 149676, 156208; CAS-SU 4219, 4229–4232, 4256–4258, 4323, 10741–10743, 11038–11041, 11044; MVZ 4913, 4914, 48013, 48015, 48016, 48042, 69691–69693, 69695–69697, 125414.

Thamnophis atratus atratus - T. a. aquaticus intergrades (64). Marin Co.: CAS 93771; MVZ 47954–47956, 47967, 47969, 68194. San Francisco Co.: MVZ 19118–19120, 19122, 19123, 19125–19128, 19133, 19134, 37138. San Mateo Co.: CAS-SU 8157, 10706, 10712; MVZ 47883–47893, 47896–47925, 93805.

Thamnophis atratus atratus (187). "San Francisco": USNM 970a (lectotype of *Eutainia atrata* and *Eutaenia infernalis vidua*). San Mateo Co.: CAS 149585–149617, 149677, 191545, 191640, 191641, 191646; CAS-SU 1198, 1200–1205, 1654, 1655, 4149, 4155, 5180, 5183, 5184, 8105, 8109–8112, 10686–10688, 10691, 10692, 10694–10696, 10698, 10827, 10828, 10831, 10833, 10834, 10897–10899, 13781, 17867, 17906, 17907, 22949–22952, 25567, 25568; MVZ 9316, 14003, 16592, 32628, 47882, 47894, 47895, 47926–47928, 92508, 187632–187636, 187654, 187655. Santa Clara Co.: CAS 54225, 191576, 191578, 191581–191583, 191596, 191598, 191599, 191602, 191609, 191613, 191617, 191620, 191622, 191624, 191625, 191633, 191635; CAS-SU 4157, 4322, 6378–6380, 8207, 8208, 13780, 18160–18162; Santa Cruz Co.: CAS 81547, 191557, 191560–191563, 191565, 191567–191569; CAS-SU 4150–4153, 7636, 7637, 10817; MVZ 26988, 35545–35553, 39443, 47935–47941, 48976–48979, 62106–62118, 100280, 149624; SJSU R4737.

Thamnophis atratus atratus - T. a. zaxanthus intergrades (25). Santa Clara Co.: CAS 191584, 191587, 191591, 191595, 191597, 191600, 191603, 191621, 191623, 191626, 191634, 191636, 191642, 191645, 191653. Santa Cruz Co.: CAS 191558, 191559, 191564, 191566, 191570–191572; CAS-SU 1675, 1679, 4148.

Thamnophis atratus zaxanthus (169). Alameda Co.: CAS-SU 4161, 11913, 11914; MVZ 1629, 2457, 3757, 10524, 12857, 24897, 24898, 24905, 24906, 25200, 32244, 38951, 38952, 47943–47948, 48538, 111370, 187622–187626, 187649, 191323. Contra Costa Co.: CAS 43695; MVZ 4009, 19139, 32885, 47949–47952, 48973–48975, 85208, 85209, 111362. Merced Co.: MVZ 39350, 39351. Monterey Co.: CAS 13764, 13765, 149553, 149554, 191541; CAS-SU 1685, 5143, 5147, 5149, 10327–10329, 11316; CPS 248; MVZ 7243, 26010, 44865, 66382, 125415. Napa Co.: CAS 191544; CAS-SU 6134, 6310–6314; MVZ 42639–42644, 47887, 47888, 47999–48008, 48010–48012, 60234, 60235, 78049–78052; 78817, 85214, 149606–149609, 149621–149623, 149625, 187630. San Benito Co.: CAS 49212, 191537–191540; MVZ 83647. San Joaquin Co.: CAS 191542; MVZ 28206, 28207. San Luis Obispo Co.: CPS 120, 188, 189, 191, 2420, 2426, 2428, 2436, 2437, 3216–3220, 3224,

3225, 3227, 3228, plus two unnumbered specimens; UCSB 15552, 21997. Santa Barbara Co.: CPS 94; UCSB 9078, 9081-9083, 13707, 14213, 17805, 17584, 18762, 22203. Santa Clara Co.: CAS 39652, 39653, 41661, 41662, CAS-SU 4091, 5852, 6520, 22953, 22954, 191574, 191575, 191577, 191579, 191580, 191585, 191586, 191588, 191590, 191592–191594, 191604–191608, 191610–191612, 191614–191616, 191618, 191619, 191628–191632, 191637–191639, 191643, 191644, 191647–191652, 195846; MVZ 79576, 207940 (holotype of *Thamnophis atratus zaxanthus*); Solano Co.: MVZ 4006–4008, 48017. Stanislaus Co.: CAS 161384, 191547–191551; MVZ 39349, 78816.

APPENDIX B

Supplemental specimens examined.— *Thamnophis atratus aquaticus* (16). Marin Co.: LSUMZ 8222–8225, 22205–22208, 34238, 34239. Sonoma Co.: LSUMZ 16531, 16638, 16644, 16648, 16649, 39069.

Thamnophis atratus atratus (20). San Mateo Co.: LSUMZ 16546, 24352–24356, 28911–28914, 28931–28933, 36936, 37905, 37907, 37908, 39599, 39600. Santa Cruz Co.: LSUMZ 16545.

Thamnophis atratus atratus - T. a. aquaticus intergrades (4). San Mateo Co.: LSUMZ 8305, 8306, 20359, 34255.

Thamnophis atratus hydrophilus (35). Shasta Co.: LSUMZ 16554, 16555, 16557, 34417, 34418, 35177, 36685, 36686, 36690–36701, 36705, 36747–36753, 39088, 39089, 40017, 40022, 40029, 46844, 46845.

Thamnophis atratus zaxanthus (23). Alameda Co.: LSUMZ 8129, 16532–16534, 16536, 16537, 16539, 16540, 34591–34593. Contra Costa Co.: LSUMZ 8131, 42815. Monterey Co.: LSUMZ 17023, 39097. San Luis Obispo Co.: LSUMZ 23907, 37189–37191, 37902. Stanislaus Co.: LSUMZ 44370, 44390, 44393.

Thamnophis elegans terrestris (42). Alameda Co.: LSUMZ 7908, 44780. Marin Co.: LSUMZ 7914. San Luis Obispo Co.: LSUMZ 55342–55346. San Mateo Co.: LSUMZ 7900–7904, 7907, 7911, 7912, 7916, 7918, 7920, 16502, 16504–16506, 16508, 16509, 19285–19291, 20356–20358, 34231, 34371, 34373, 40248. Santa Cruz Co.: LSUMZ 13536. Sonoma Co.: LSUMZ 16636, 34374.

APPENDIX C

Character support for the phylogenetic tree.— The ingroup clade, comprising southern populations of *Thamnophis atratus*, was supported by shorter SVL (<415.3 mm vs. 466.5 mm [mean values, and hereafter]), fewer ventrals (<161.1 vs. 164.2), fewer subcaudals (<83.8 vs. 86.6), fewer ASR (<19.6 vs. 20.2), fewer PSR (<16.1 vs. 16.9), broader interorbital width (>0.39 vs. 0.38), broader MVSW (>1.9 vs. 1.7), STR value either greater than 4.9 or less than 3.9 (vs. 4.3), longer PCS (<0.80 vs. 0.83), greater eye diameter (>0.18 vs. 0.17), more maxillary teeth (>24.5 vs. 23.6), male/female SVL ratio either greater than 0.81 or less than 0.91 (vs. 0.86), greater ML/FL ratio (<0.70 vs. 0.85), lesser FL/PL ratio (>0.97 vs 0.92), greater LDL/LVL ratio (<0.66 vs. 0.71), and PRF/INL ratio either greater than 1.01 or less than 1.11 (vs. 1.08).

The branch leading to A, D is supported by lower STR value (<3.9 vs. 5.0), and higher pupil/eye ratio (0.47 vs. <0.45). The clade (G (B, F)) is supported by greater STR value (4.9 vs. <3.9) and more maxillary teeth (25.6 vs. <24.8). The clade (B, F) is supported by more V (>159.5 vs. 153.3), narrow interorbital (0.39 vs. 0.40), and lower pupil/eye ratio (0.43 vs. 0.45).

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